

## Femoral Anatomy of *Aegyptopithecus zeuxis*, An Early Oligocene Anthropoid

FRIDERUN ANKEL-SIMONS,<sup>1</sup> JOHN G. FLEAGLE,<sup>2\*</sup>  
AND PRITHIJIT S. CHATRATH<sup>1</sup>

<sup>1</sup>Duke University Primate Center, Durham, North Carolina

<sup>2</sup>Department of Anatomical Sciences, Health Sciences Center,  
State University of New York, Stony Brook, New York

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**ABSTRACT** Three partial femora from Quarries I and M of the early Oligocene Jebel Qatrani Formation in the Fayum of Egypt are attributed to *Aegyptopithecus zeuxis* on the basis of their appropriate size and anthropoid morphology. Compared with extant catarrhines, *Aegyptopithecus* is unusual in having a distinct gluteal tuberosity (third trochanter) and a relatively deep distal femoral articulation. In the estimated neck angle, *Aegyptopithecus* resembles arboreal quadrupeds rather than either leaping or suspensory primates. It seems likely that the femur of this species was relatively robust and short for its body mass. In aspects of its femoral anatomy, *Aegyptopithecus* is quite different from the parapihtheid *Apidium* and more similar to *Catopithecus* from late Eocene deposits of the Fayum, and also to small hominoids from the Miocene of East Africa. Am J Phys Anthropol 106:413–424, 1998. © 1998 Wiley-Liss, Inc.

*Aegyptopithecus zeuxis* is an early catarrhine from the upper (early Oligocene) levels of the Jebel Qatrani Formation in the Fayum Province of Egypt. As a basal catarrhine that precedes the divergence of Old World monkeys and apes, *Aegyptopithecus* is particularly important for understanding the primitive morphology of Old World higher primates that gave rise to the modern groups of catarrhines. Since its initial description in 1965, *A. zeuxis* has become one of the best known of all fossil primates on the basis of cranial and dental remains (e.g., Simons, 1967, 1987; Kay et al., 1980; Fleagle and Kay, 1983).

In contrast with the abundant documentation of the dental and cranial morphology of this species, postcranial remains are limited (Gebo, 1993; Simons, 1995). The forearm of *A. zeuxis* is relatively well known from several humeri and ulnae (Fleagle et al., 1975; Conroy, 1976; Fleagle and Simons, 1982). However, the only hindlimb remains described thus far are several calcanei and tali

(Gebo and Simons 1987; Fleagle 1983) and some recently described pedal phalanges (Hamrick et al., 1995).

In this article, we report on three partial femora from Quarries I and M of the Jebel Qatrani Formation and make preliminary comparisons to femora in a range of living and fossil anthropoids in order to evaluate the fossil femora's functional and phylogenetic significance. These remains provide the first documentation of the femur in this early catarrhine.

### DATING AND ALLOCATION OF FOSSILS

Two of the femoral remains (DPC 5262 and 8709) are from Quarry I. A femoral shaft including the lesser trochanter (DPC 2480) is from Quarry M. Quarries I and M are in

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\*Correspondence to: John G. Fleagle, Department of Anatomical Sciences, Health Sciences Center, State University of New York, Stony Brook, NY 11794.

E-mail: JFLEAGLE@mail.som.sunysb.edu

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TABLE 1. Estimated weights of primates from Quarries I &amp; M, Jebel Qatrani Formation

Taxon	Est. Mass (g)	95% con.	Source
<i>Aegyptopithecus zeuxis</i>	5,876	5,346–6,450	Kay and Simons, 1980
	5,281	4,349–6,216	Kay and Simons, 1980
	7,500		Gingerich, 1977
	5,600		Gingerich, 1977
	6,495	5,935–7,110	Gingerich et al., 1982
	6,035	5,620–6,480	Gingerich et al., 1982
	6,708		Conroy, 1987
	6,716		Conroy, 1987
	6,079		Conroy, 1987
	2,951	2,698–3,228	Kay and Simons, 1980
<i>Propliopithecus chirobates</i>	4,195	3,845–4,570	Gingerich et al., 1982
	3,929	3,660–4,195	Gingerich et al., 1982
	4,266		Conroy, 1987
	4,257		Conroy, 1987
	3,624		Conroy, 1987
<i>Parapithecus grangeri</i>	1,802		Kay and Simons, 1980
	2,995	2,790–3,215	Gingerich et al., 1982
	3,171		Conroy et al., 1987
	3,161		Conroy, 1987
	2,582		Conroy, 1987
<i>Parapithecus cf. fraasi</i>	1,700		
<i>Apidium phiomense</i>	1,177	1,051–1,318	Kay and Simons, 1980
	1,675	1,535–1,830	Gingerich et al., 1982
	1,698		Conroy, 1987
	1,687		Conroy, 1987
	1,265		Conroy, 1987
<i>Qatrania fleaglei</i>	500		
<i>Afrotarsius chatrathi</i>	100		
?lorisoid	100		

the upper part of the Jebel Qatrani Formation. They are separated by only 50 meters of stratigraphic section and are virtually equivalent in time (Bown and Kraus, 1988). These quarries have yielded almost identical faunas and there are no significant differences between samples of the primates found in the two quarries. The exact age of the Jebel Qatrani Formation is the subject of considerable debate. The formation is capped unconformably by a basalt that was originally dated by whole rock  $^{40}\text{K}$ - $^{40}\text{Ar}$  dating at 31 MYA (Fleagle et al., 1986), but has recently been redated by single-crystal  $^{40}\text{Ar}$ - $^{39}\text{Ar}$  dating at 23.64 MYA (Kappelman et al., 1992). Because of the unconformity between the underlying sediments and the dated basalt, the lack of other radiometric dates from the formation, and the absence of good faunal correlations with other well-dated deposits, various researchers have provided different estimates of the age of this formation. Van Couvering and Harris (1991) argued that the entire Jebel Qatrani Formation is Eocene in age; Gingerich (1993) argued that the entire formation is Oligocene. The most widely accepted estimate,

however, is that of Kappelman et al. (1992), which is based on paleomagnetic correlations that place the upper part of the Jebel Qatrani Formation at approximately 33 MYA, or early Oligocene.

The fossils discussed here are attributed to *A. zeuxis* on the basis of size and morphology. They are clearly primate skeletal elements, as they differ from femora of the few other mammals from these quarries that are in the same general body size, such as hyracoids or creodonts. These femora are most suitable for *A. zeuxis* based on its estimated body size. Table 1 lists the fossil primates that have been described from Quarries I and M and their estimated body mass generated from dental or cranial dimensions by various authorities. *A. zeuxis* is the only large anthropoid known from quarries I and M. The next largest primate species, *Parapithecus grangeri* and *Propliopithecus chirobates* are approximately two-thirds to one-half the size of *A. zeuxis*, and the most common species, *Apidium phiomense*, is less than one-fourth the estimated size of *A. zeuxis* (Table 1).

We used a regression of body mass on femoral midshaft circumference to estimate the size of the species to which the fossil femora are best attributed. A sample of 40 primate species ranging in size from less than 1 kg to over 50 kg yields the following least squares regression equation (L. Godfrey, personal communication; see Godfrey et al., 1991):

$$\ln(\text{body mass}) = -8.527 + 2.94[\ln(\text{femoral midshaft circumference})]$$

Because the fossils lack complete proximal and distal ends, and in one specimen the shaft was crushed and has been restored, the measures of midshaft circumference are necessarily estimates. The average midshaft circumference for the three femora yields an estimated body mass of 6,708 g. Of the Fayum primates, *A. zeuxis* is closest to this body size and this estimate overlaps with many estimates of the size of this species based on dental dimensions (Table 1).

Figure 1 compares the most complete of the fossil femora (DPC 5262) with a femur of *Chiropotes satanas*, an extant platyrrhine similar in body size to *Propithecus chiobates* or *Parapithecus grangeri* (body mass approximately 3,000 g), and a femur of *Presbytis melalophos*, an extant catarrhine similar to the estimated size of *A. zeuxis* (body mass approximately 7,000 g). Although the fossil femur is only slightly longer than the femur of *Chiropotes*, in shaft robustness and in the size of the preserved portions of the proximal and distal ends it is more comparable to the bone of the 7 kg leaf monkey. Thus, although there is no direct association between the fossil femora and any cranial or dental remains of a primate species, all size criteria indicate that the femora are best allocated to *Aegyptopithecus*.

#### DESCRIPTION AND COMPARISON OF FOSSILS DPC 5262

DPC 5262 is the most complete of the three femora (Figs. 2B, 3B). It is a right femur. The shaft has been crushed and restored and there are puncture marks indicating predator behavior. Although most of

the bone is preserved in gross morphology, the crushing caused considerable damage to the diaphysis. In addition, much of the outer table of cortical bone is missing from the external surface of the fossil, precluding exact measurements of many standard biometrical dimensions or identification of muscle scars. Nevertheless, general proportions and many morphological features are clearly preserved.

In the absence of both the femoral head and the proximal part of the greater trochanter, we took a surrogate measure of femoral length from the proximal surface of the femoral neck where it joins the medial aspect of the greater trochanter to the distal-most projection of the femoral condyles. This reduced femoral length is approximately 142 mm in DPC 5262. Although the greater trochanter and the articular surface of the head are both missing, and among primates the greater trochanter can show a wide range of projection, it appears that much of the subarticular part of the femoral head is present in this fossil, with less than 10 mm missing. On this basis, we estimate the functional length of the femur (femoral head to distal condyles) at approximately 150 mm. This is slightly larger than the same dimension in *Cebus apella* or *Chiropotes satanas* and substantially smaller than the same dimension in *Alouatta seniculus* or *Presbytis melalophos*—animals with a body mass similar to that estimated for *A. zeuxis* based on dental and cranial dimensions (Fig. 1; Table 2).

While the absence of the femoral head and erosion of part of the neck precludes a precise measurement of the neck (collo-diaphysis) angle, our best estimate indicates an angle of 120–130°. The femoral neck angle is notoriously difficult to measure in an accurate, reproducible fashion and may show considerable intraspecific variation. Nevertheless, there are several well-documented patterns in the distribution of reported femoral neck measurements according to locomotor adaptations among living primates and other mammals (Anemone, 1990; Fleagle, 1977, 1988; Fleagle and Meldrum, 1988; Fleagle and Simons, 1995; Gebo et al., 1994; Junger, 1980; White, 1993) (Table 3). Femoral neck angles among lea-



Fig. 1. Anterior view of the right femur of three anthropoids: *Chiropotes satanas* (left), *Aegyptopithecus zeuxis*, DPC 5262 (middle), and *Presbytis melalophos* (right). All bones approximately natural size. Note that the fossil femur is only slightly longer than the femur of the bearded saki, but that the breadth of the proximal and distal regions and the shaft diameter are more similar in size to the larger leaf monkey.

ing primates (e.g., *Indri*, *Pithecia pithecia*, *Presbytis melalophos*, *Nasalis*) are generally relatively low. In contrast, primates (and edentates, see White, 1993) that engage in considerable hindlimb suspension (e.g.,

*Pongo*, *Symphalangus*, *Ateles*, *Chiropotes*) tend to have the highest femoral neck angles. The estimated neck angle for *Aegyptopithecus* falls between these extreme values and this can also be seen in Figure 1.



Fig. 2. Anterior view of three femoral remains attributed to *Aegyptopithecus zeuxis*. **A** = DPC 8709; **B** = DPC 5262; **C** = DPC 2480. Approximately natural size.

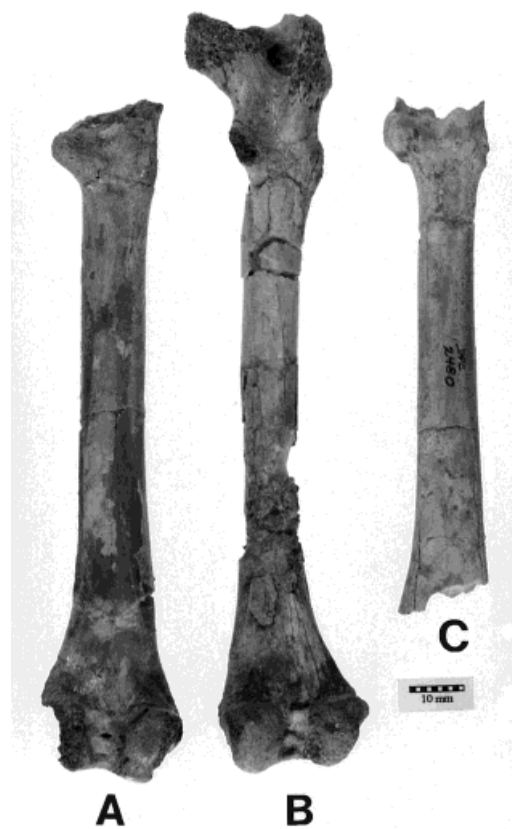


Fig. 3. Posterior view of three femoral remains attributed to *Aegyptopithecus zeuxis*. **A** = DPC 8709; **B** = DPC 5262; **C** = DPC 2480. Approximately natural size.

The estimated neck angle for *Aegyptopithecus* is most comparable to that of many quadrupedal anthropoids. It is also similar to values reported for *Proconsul* and other early Miocene apes (Rose et al., 1992). The weathering of the cortical surface precludes accurate measurement of the dimensions of the femoral neck or any determination on the presence or absence of a tubercle on the femoral neck as found in many primates (e.g., Rose et al., 1992; Ford, 1986).

The most proximal part of the greater trochanter is missing. In anterior aspect, the proximal part of the femur is relatively broad, with the lateralmost projection of the greater trochanter extending well beyond the lateral margin of the shaft. This is similar to the condition found in parapithecids, *Catopithecus*, most platyrrhines except

atelines, and many Miocene apes. The greater trochanter also shows a slight anterior overhang anterior to the surface of the shaft and neck, but does not show an "excavated" appearance for an enlarged *m. vastus lateralis* as in many leaping primates (Fleagle and Meldrum, 1988; Fleagle and Simons, 1995). There is no evidence of an intertrochanteric line, as the outermost table of bone is missing.

The lateral surface of the greater trochanter is relatively broad and flattened in the sagittal plane, as in many platyrrhines, but more so than in most Miocene hominoids (Rose et al., 1992), and less than the broad surface found in parapithecids (Fleagle and Simons, 1995). On the lateral surface of the bone where the greater trochanter joins the shaft, at approximately the level of the



TABLE 2. Shaft and articular dimensions of *Aegyptopithecus zeuxis* compared with selected extant and fossil primates

Taxon (n)	Maximum length (mm)	AP diameter at midpoint	BL diameter at midpoint (mm)	Midpoint circum. (mm)	Distal Articular AP Distal Articular ML (mm)
<i>Aegyptopithecus zeuxis</i>					
DPC 5262	150.0	10.0	12.0	34	.83
DPC 2480		10.0	10.7	33	
DPC 8709		12.0	12.6	37.2	
<i>Pliopithecus</i> (Ind. II)	206.0	10.5	11.5		.76*
<i>Dendropithecus macinnesi</i> (KMN-SO 1005)					.86*
<i>Proconsul nyanzae</i>					
KNM-MW 13142	295.0**	19.4**	20.6**		.73*
<i>Alouatta seniculus</i> (8)					
mean	161.69	9.73	11.41		.75
std	10.21	0.70	0.90		.03
<i>Hylobates hoolock</i> (5)					
mean	192.70	10.12	10.86		.67
std	10.26	0.52	0.51		.02
<i>Presbytis melalophos</i> (9)					
mean	191.10	10.40	10.73		.82
std	5.30	0.45	0.34		.76
<i>Cercopithecus denti</i> (4)					
mean	143.08	8.93	8.85		.85
std	11.75	0.70	0.92		.003
<i>Callicebus moloch</i> (4)					
mean	90.93	4.83	5.43		.79
std	1.62	0.16	0.23		.02
<i>Cebus apella</i> (4)					
mean	133.63	8.73	8.53		.74
std	3.68	0.35	0.25		.02
<i>Varecia vareigata</i> (4)					
mean	143.70	9.28	9.10		1.00
std	2.32	0.32	0.32		.0005

\* From Rose et al., 1992.

\*\* From Ward et al., 1993.

distal end of the lesser trochanter, is a prominent gluteal tuberosity or third trochanter (e.g., HersHKovitz, 1987) for the insertion of *m. gluteus superficialis*, a feature normally absent in modern catarrhines and parapithecids, but found in some small platyrrhines. The size, shape, and even identification of the third trochanter is a source of considerable disagreement in primate comparative anatomy (see HersHKovitz, 1987; Ford, 1980, 1988; reviewed in Gebo et al., 1994; Dagosto and Schmid, 1996). The third trochanter in *Aegyptopithecus* is not a prominently projecting process, as in many extant and fossil prosimians (e.g., Gregory, 1920); it is a small but distinct projection, as in *Aotus* (also *Homunculus*) and more developed than the simple ridge-like gluteal tuberosity found in many platyrrhines (e.g., callitrichines, pitheciines) and most catarrhines. The third trochanter/gluteal tuberosity in *Aegyptopithecus* is intermediate in size between the more prosimian-like process found in *Cato-*

*pithecus* (Gebo et al., 1994) and the ridge-like tuberosity found in some small Miocene hominoids (e.g., KNM-SO 1011, attributed to *Limnopithecus evansi*; Harrison, 1982; Rose et al., 1992) (Fig. 3).

On the dorsal surface, the trochanteric fossa is relatively deep. Like the third trochanter, the development of crests surrounding the trochanteric fossa, and the terminology used to describe these crests, differs considerably among living primates and among primatologists (see Gebo et al., 1994; Rose et al., 1992). In most prosimians, many platyrrhines, and *Apidium* the posterior crest of the greater trochanter forms the lateral wall of the trochanteric fossa and then extends distally before fading out at the lateral edge of the femoral shaft. In *Apidium* (and sometimes in *Aotus* and *Saguinus*) the distal crest of the (large) lesser trochanter extends laterally to join the distal extension of this paratrochanteric crest and delimits the inferior border of the tro-

TABLE 3. Measurements and ranges of the femoral neck angle in some Old and New World primates

Taxon (N)	Femoral Neck Angle		Source
	X	Range	
<i>Aegyptopithecus</i> (DPC 5262)		120°–130°	estimated
<i>Apidium phiomense</i> (4)	116.5°	114°–120°	Fleagle and Simons, 1985
<i>Simiolus</i> (KNM-WK 18117)	130°		Rose et al., 1992
<i>Pliopithecus</i> (Ind. II)	130°		Rose et al., 1992
<i>Limnopithecus</i> (KNM-SO 1011)	128°		Rose et al., 1992
<i>?Rangwapithecus</i> (KNM-SO 399)	133°		Rose et al., 1992
<i>Proconsul nyanzae</i> (KNM-MW 13142)	131°		Rose et al., 1992
<i>Indri indri</i>		100°–105°	Jungers, 1978
<i>Aotus</i> (7)	123°	120°–126°	Halaczek, 1972
<i>Callithrix</i> (14)	127°	120°–130°	Halaczek, 1972
<i>Saimiri</i> (13)	127°	123°–129°	Halaczek, 1972
<i>Ateles</i> (7)	136°	134°–138°	Halaczek, 1972
<i>Pithecia pithecia</i> (11)	106°	99°–111°	Fleagle and Meldrum, 1988
<i>Chiropotes satanas</i> (6)	137°	134°–140°	Fleagle and Meldrum, 1988
<i>Cercopithecus</i> (10)	117°	110°–122°	Halaczek, 1972
<i>Macaca</i> (16)	123°	118°–127°	Halaczek, 1972
<i>Nasalis</i> (4)	115°	115°–116°	Halaczek, 1972
<i>Hylobates</i> (16)	130°	120°–139°	Halaczek, 1972
<i>Symphalangus</i> (7)	136°	132°–141°	Halaczek, 1972
<i>Pongo</i> (14)	142°	132°–158°	Halaczek, 1972
<i>Pan</i> (10)	135°	121°–141°	Rose et al., 1992

chanteric region (including the fossa and the lateral surface of the lesser trochanter). In many platyrrhines (e.g., *Chiropotes*, *Cacajao*; see Rose et al., 1992) the crests of the lesser trochanter end more medially and the posterior crest of the greater trochanter lies laterally so the region is “open” inferiorly (terminology of Gebo et al., 1994), although there may be a smaller crest more proximally that delimits the inferior border of the trochanteric fossa (terminology of Rose et al., 1992). In many large platyrrhines and most catarrhines, including humans, the posterior crest of the greater trochanter forms the medial wall of the greater trochanter on the posterior surface and then extends distomedially to join the lesser trochan-

ter to form an intertrochanteric crest. There is considerable variation in whether this intertrochanteric crest abuts the proximal or distal part of the lesser trochanter. This crest also varies considerably in strength at its distal end. Moreover, there is often an additional smaller crest more proximally that delimits the inferior edge of the trochanteric fossa (Rose et al., 1992). In DPC 5262, the intertrochanteric crest is quite distinct, oriented distomedially and extends distally as far as the base of the lesser trochanter. It most closely resembles the morphology of this region in several large platyrrhines and, to a lesser extent, Old World monkeys. The development of the intertrochanteric crest in Miocene apes is variable (e.g., Rose et al., 1992). In all there is an obliquely oriented intertrochanteric crest, but the development of the crest is quite variable. Some species show a development of the crest similar to that in DPC 5262. In others, the distal half of the crest becomes relatively indistinct well before it reaches the level of the lesser trochanter.

In *Aegyptopithecus*, the trochanteric fossa is open distally, as in many platyrrhines and Miocene hominoids. This contrasts with the condition seen in many Old World Monkeys in which the intertrochanteric crest joins the top of the lesser trochanter, and the unusual condition found in parapithecids (and in *Microchoerus*) in which it joins the expanded lower border of the lesser trochanter (Fleagle and Simons, 1995; Dagosto and Schmid, 1996; Gebo et al., 1994).

In *Aegyptopithecus*, the broken lesser trochanter is a relatively long process and seems comparable to that structure in most Miocene hominoids. It differs from the broad, plate-like process found in parapithecids (Gebo et al., 1994; Fleagle and Simons, 1995). Due to the fragmentary nature of the fossils, we have been unable to measure the projection angle of the lesser trochanter (e.g., Gebo et al., 1994; Dagosto and Schmid, 1996).

Compared with most extant primates, the portion of the femur of *Aegyptopithecus* proximal to the base of the lesser trochanter, including the greater and lesser trochanters, comprises a much larger portion of total femoral length (see Fig. 1). Thus, the

distance from the top of the femoral neck to the distal end of the greater trochanter is approximately 23% of reduced femoral length in *A. zeuxis*. This is similar to the proportions found in parapithecids or *Homunculus*, but greater than the relative distance in most extant primates.

The diaphysis of DPC 5262 is shattered, with part of the cortical bone missing, but nevertheless permits reconstruction of its total length and minimum estimations of the midpoint dimensions (Table 2). In cross-sectional shape, the diaphysis is slightly ovoid anteroposteriorly in the proximal one-third and becomes almost triangular in its distal third. The anterior aspect of the distal third of the femur is bluntly ridged. The ridge constitutes the tip of the triangular cross-section of the distal part of the shaft. Distally, the ridge becomes flat and spreads out into the proximal part of the patellar groove that is eroded away.

The distal part of the diaphysis shows a gradual broadening from the diaphysis to the epicondyles (Figs. 2, 3). This is most similar to the condition found in extant apes, and many fossil catarrhines, including *Pliopithecus* and Miocene hominoids (e.g., *Proconsul* and KNM SO 1005, cf. *Dendropithecus macinnesi*; Ward et al., 1993; Rose et al., 1992) and contrasts with the more abrupt flaring at the distal epiphysis in *Alouatta* and many cercopithecoids (see Fig. 1).

Even though the distal articular surfaces of the femur are somewhat abraded, it is possible to make a reasonable estimate of overall proportions. The maximum mediolateral width of the distal articulation is 27.4 mm. The estimated anteroposterior depth is approximately 22.5 mm. This is a minimum estimate since the patellar surface is abraded in DPC 5262. These dimensions yield a height to width index of 0.83 for *A. zeuxis*, which is relatively deep for extant anthropoids, especially hominoids, but similar to the proportions found in some *Cercopithecus* and in the distal femoral articulation of small Miocene hominoids from Kenya (KNM SO 1005, cf. *Dendropithecus macinnesi* = 0.86; Rose et al., 1992). The anterior aspect of the patellar articular surface has eroded away in such a manner that it only preserves the outline of the original *facies patellaris*. This *facies patellaris* appears to be

comparatively high, but relatively broad. This is most comparable to the proportions seen in extant hominoids, many platyrrhines, and Miocene hominoids. The patellar groove is narrower and deeper in cercopithecoids (e.g., Rose, 1993; Ward et al., 1995). There is too much erosion to determine if there was a prominent lip on either side of the patellar surface.

The femoral condyles and intercondylar notch are relatively well preserved except for some erosion on the edges of the condylar surfaces. There is no evidence of any pronounced asymmetry in condyle size or any "splaying" of the medial condyle, as is found in many suspensory anthropoids, including *Ateles*, extant hominoids, and *Proconsul* (Rose, 1993). Between the lateral condyle and the lateral epicondyle there is a pronounced groove for the lateral collateral ligament.

#### DPC 8709

The partial right femur DPC 8709 (Figs. 2A, 3A) from Quarry I preserves a virtually complete and undistorted diaphysis from the lesser trochanter to the distal articulation and much of the lateral condyle. The entire head, neck, and greater trochanter are missing, as is the medial condyle. This femur is similar in size to DPC 5262. The length of DPC 8709 from the middle of the lesser trochanter to the distal end of the femoral condyles is 119 mm (compared with 117 mm for DPC 5262). The lesser trochanter is nearly complete. It is a relatively broad process. The gluteal tuberosity (third trochanter) is less well developed than in DPC 5262. The diaphysis of DPC 8709 is roughly circular in shape, with a flattened posterior surface. It appears somewhat more robust than that of DPC 5262 with trochanter-condyle midpoint dimensions of 12.1 mm (a-p) and 12.3 mm (m-l). The diaphysis is slightly bowed in a proximal to distal direction with an anterior convexity. The distal articular surface is poorly preserved, but appears to be similar to that described for DPC 5262, with the same pronounced groove for the lateral collateral ligament.

#### DPC 2480

This specimen, from Quarry M, preserves most of the diaphysis from the top of the



lesser trochanter to the distal broadening just proximal to the distal articulation (Figs. 2C, 3C). The total length of the specimen is 97 mm. It is slightly smaller than the other specimens, judging from the distance from the lesser trochanter to the distal broadening; however, there are no precise landmarks available for exact comparisons. As in DPC 8709, the lesser trochanter is a broad process. The gluteal tuberosity (third trochanter) is a prominent ridge similar to that in DPC 5262. As in DPC 8709, the diaphysis is slightly bowed anteriorly and has the cross-sectional shape of a slightly flattened circle.

### DISCUSSION AND CONCLUSIONS

These three new fossils, despite their fragmentary condition, provide considerable information about the femoral anatomy of an early catarrhine that can be used for both functional and phylogenetic interpretations. The estimated maximum length of the most complete femur is 150 mm and the other two specimens are probably within 10% of this length. The two most complete humeral specimens of *A. zeuxis* have a mean length of 141 mm (Fleagle and Simons, 1982). This gives a humero-femoral index of 94. This value is well above that of leaping prosimians and most colobines and below that of gibbons, great apes, and *Ateles*. The estimated intermembral index for *A. zeuxis* is similar to values for *Alouatta* and many other arboreal, quadrupedal primates (Table 4).

The estimated angle of the femoral neck (120–130° degrees) groups *Aegyptopithecus* with quadrupedal monkeys. It shows no evidence of a proximally directed neck, as in suspensory primates, or a short neck set perpendicular to the shaft, as seen in most leapers (Table 3; see discussions by Anemone, 1990; Dagosto and Schmid, 1996; Fleagle and Meldrum, 1988; Fleagle and Simons, 1995; White, 1993; and references therein). Likewise, although there is a relatively expanded greater trochanter, there is no evidence of an extensive excavation of the anterior surface for the origin of *m. vastus lateralis* on the proximal part the femur, as seen in most leaping prosimians and *Apidium* (e.g., Anemone, 1990; Fleagle and Simons, 1995). Similarly, the distal articular

TABLE 4. Humero-femoral Index measurements in some Old and New World primates

Taxon	Humero-femoral Index		Range
	$\bar{x}$	SD	
<i>Aegyptopithecus zeuxis</i> (est)	94		
<i>Apidium phiomense</i> (est)	62		
<i>Microcebus rufus</i> (6)	72.5	0.9	
<i>Cheirogaleus major</i> (10)	72.9	2	
<i>Hapalemur griseus</i> (20)	60.7	3	
<i>Varecia variegata</i> (17)	70.6	1.9	
<i>Avahi laniger</i> (16)	48.8	1.5	
<i>Indri indri</i> (16)	54.4	1.7	
<i>Galagoides demidoff</i> (18)	66.1	2	
<i>Otolemur crassicaudatus</i> (11)	65.8	1.6	
<i>Arctocebus calabarensis</i> (21)	84.2	2.1	
<i>Perodicticus potto</i> (20)	85.6	3.7	
<i>Cebuella pygmaea</i> (13)	88.6	1.6	
<i>Leontopithecus rosalia</i> (10)	89.2	1.4	
<i>Samiri sciureus</i> (9)	82.4	1.7	
<i>Cebus capucinus</i> (3)	82	3	81–83
<i>Alouatta seniculus</i> (2)	97		97–97
<i>Lagothrix lagothricha</i> (8)	99.8	1.7	
<i>Procolobus verus</i> (3)	81.5		
<i>Presbytis entellus</i> (2)	70		70–71
<i>Nasalis larvatus</i> (6)	87.3	1.9	
<i>Miopithecus talapoin</i> (8)	85.2	1.2	
<i>Cercopithecus sabaeus</i> (5)	82		79–89
<i>Macaca fascicularis</i> (6)	86		82–89
<i>Papio anubis</i> (11)	90.1	2	
<i>Hylobates lar carpenteri</i> (30)	115	2.7	
<i>Hylobates syndactylus</i> (17)	128.5	4.1	
<i>Pan paniscus</i> (10)	97.6	2	
<i>Gorilla gorilla</i> (21)	117.2	2.9	

Data from Jungers (1985), Zapfe (1960), and Fleagle and Simons (1995).

region of the femur of *Aegyptopithecus* is most comparable to that of anthropoid arboreal quadrupeds. It is shallower than the distal articular region of leaping prosimians and the early anthropoid *Apidium* (Ford, 1980; Anemone, 1990; Fleagle and Simons, 1995) but relatively deeper and less broad than the region in more suspensory hominoids, sloth lemurs, or sloths (e.g., Fleagle and Simons, 1995; Godfrey, 1988; White, 1993).

Thus, the overall proportions of the femur suggest that this species was a robust arboreal quadruped. This is very similar to locomotor reconstructions based on other limb elements (for reviews, see Fleagle, 1988; Gebo, 1993; Simons, 1995). Fleagle et al. (1975) and Conroy (1976) argued that the ulna of *Aegyptopithecus*, with its long olecranon and anteroposteriorly deepened shaft, was that of a heavily built slow-moving arboreal quadruped similar to *Alouatta* or *Varecia*. Fleagle and Simons (1982) described the humerus of *Aegyptopithecus* as

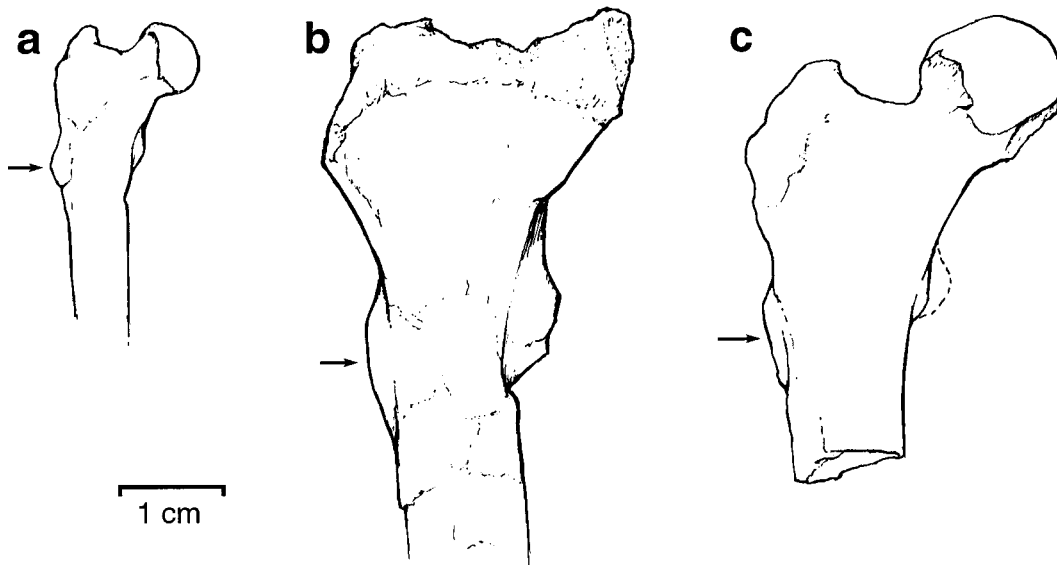


Fig. 4. Anterior view of the proximal part of the femur of **a)** *Catopithecus browni*; **b)** *Aegyptopithecus zeuxis*; **c)** *Limnopithecus evansi* (KNM-SO 1001), a small proconsulid. Arrow indicates gluteal tuberosity or third trochanter.

that of a robust arboreal quadruped that lacked characteristic features of either suspensory primates, terrestrial quadrupeds, or clinging species. Most recently, Hamrick et al. (1995) concluded that the manual and pedal phalanges attributed to *A. zeuxis* showed adaptations for powerful grasping and indicated that this species was an arboreal quadruped.

Although the finding that the femur of *Aegyptopithecus* resembles that of arboreal quadrupeds is not a surprising discovery, it is in accordance with reconstructions of the locomotor habits of this early anthropoid based on other attributed limb elements and serves as corroborative evidence for earlier interpretations. Likewise, although it has been widely argued that arboreal quadrupedalism is probably something of a baseline locomotor behavior for primates and for early anthropoids (e.g., Fleagle, 1988; Gebo, 1993), the anatomy of the femur of *A. zeuxis* and the reconstructed locomotor behavior of this species are strikingly different from the femoral anatomy and reconstructed locomotor adaptations of its contemporary, *Apidium phiomense*. This latter species shows striking adaptations for leaping in many aspects of its femoral anatomy, and has perhaps the

most distinctive and specialized femoral anatomy of all anthropoids (Fleagle and Simons, 1995).

Indeed, comparison of the femoral anatomy of *Aegyptopithecus* with that of *Apidium* highlights the fact that these femora of *Aegyptopithecus* also provide valuable information for reconstructing the phylogeny of early anthropoids (e.g., Gebo et al., 1994; Kay et al., 1997). Overall, the femur of *Aegyptopithecus* is strikingly different from that of parapithecids and lacks all of the unique features characteristic of parapithecoid femora, including the quadrate, often posteriorly directed lesser trochanter and prominent continuous crest between the base of the lesser trochanter and the paratrochanteric crest that walls off the trochanteric region inferiorly (e.g., Gebo et al., 1994; Fleagle and Simons, 1995; see also Dagosto, 1993; Dagosto and Schmid, 1996). Rather, the femur of *Aegyptopithecus* is more similar to that of *Catopithecus* (Gebo et al., 1994) and to some small Miocene hominoids from East Africa (Rose et al., 1992) in the morphology of the greater trochanter, the trochanteric cresting, the lesser trochanter, and the gluteal tuberosity (Fig. 4). Thus, although a third trochanter or prominent gluteal tuber-

osity is uncommon among extant catarrhines, this feature in *Aegyptopithecus* is almost exactly intermediate between the large, almost prosimian-like process found in *Catopithecus* (Gebo et al., 1994) and the prominent tuberosity in KNM-SO 1001 (*Limnopithecus evansi*), a small Miocene hominoid from East Africa. In addition, although the distal articulation of the femur of *Aegyptopithecus* resembles other anthropoids (except *Apidium*) in being relatively broader than deep, this articulation is deeper than that of many later catarrhines and similar to small "apes" from the early Miocene of East Africa (e.g., *Dendropithecus macinnesi*—KNM-SO 1005). A relatively deep distal femoral articulation may be the primitive condition for early catarrhines as it is for anthropoids (Fleagle and Kay, 1987). Thus, the new evidence from the femur supports interpretations from other aspects of its anatomy that *Aegyptopithecus* is a basal catarrhine with numerous primitive features, some of which are also retained by extant platyrrhines. Overall, *Aegyptopithecus* is intermediate in many aspects of femoral anatomy between the more primitive oligopithecines from the late Eocene of the Fayum and the early Miocene proconsulids from East Africa.

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